

Chapter 5

How to Measure Animal Personality and Why Does It Matter? Integrating the Psychological and Biological Approaches to Animal Personality

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5.1 Introduction: What Is Animal Personality?

During the last few years individual differences in nonhuman animal (hereafter “animal”) behavior have been a subject of rapidly growing research interest (reviews in Réale et al. 2007; Sih and Bell 2008). This has met the much older research tradition of personality psychology, which includes human and, more recently, animal personality (Gosling 2001). Individual differences in behavior and their underlying psychology are now increasingly relevant research fields in several species of animals.

Individuals in many species, from invertebrates to lizards, fish, birds, and mammals, differ in their behavior from each other. This variation is often temporally consistent, meaning that an individual’s general behavioral tendency stays similar over time (Sih et al. 2004b). Behavioral tendencies generalize to some extent across situations, so an individual shows limited plasticity in its responses (Sih et al. 2004a, b). Behavioral tendencies are heritable (van Oers et al. 2005), have significant fitness consequences (Smith and Blumstein 2008), and may be organized hierarchically so multiple traits correlate to form higher organizational levels (Réale et al. 2007; Sih and Bell 2008). Consistent behavioral variation can be named “personality,” following the human personality psychology research tradition. Also, other terms (e.g., temperament, coping style, behavioral syndrome) have been applied to consistent interindividual behavioral variation, each having its own particular connotation (Réale et al. 2007; Sih and Bell 2008). In this chapter, however, I treat them as synonyms and define personality as consistent interindividual variation in behavior. With this definition, I take no stand regarding the proximate-level mechanisms, including psychological ones, underpinning behavior.

Consistent variation in behavior is evolutionarily puzzling because natural selection would be expected to winnow out any variation that has fitness consequences, so

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that over time the optimally adaptive level of a behavioral trait would be the prevailing phenotype in a population. For example, if bold individuals locate food faster than shy individuals, bolder individuals could be expected to have higher fitness and thus, in time, boldness should be favored over shyness. Consistency in behavior is also challenging to understand because it limits an individual's flexibility to adjust its behavior to deal with a situation in an optimal way. Moreover, behavioral variation often occurs in suites of correlated behaviors; for example, individuals that are relatively bolder are also relatively more aggressive (Sih and Bell 2008), evoking questions about why such covariation should exist.

The booming research on animal personality applies various approaches and methodologies. There has been much debate over how to best assess animal personalities (e.g., Gosling and Vazire 2002; Itoh 2002; Réale et al. 2007; Vazire et al. 2007; Uher and Asendorpf 2008). In this chapter, two fields of animal personality research are discussed – psychological and biological – that drastically differ from each other in their approaches. However, despite the seemingly fundamental differences, common ground can be found. Although their particular paradigms may differ, the aims of the two approaches are in the end similar: to map the depth and width of individual differences in behavior; to understand the structure of this variation; to understand its evolutionary consequences and underlying mechanisms; and to facilitate predictions, which in turn are helpful in a broad range of applications. Indeed, several researchers have stressed the benefits of such integration (Gosling 2001; Nettle 2006; Sih and Bell 2008; Uher 2008a; Brosnan et al. 2009). To achieve integration and synergy, we need to understand each other's approaches and their conceptual and practical consequences. Therefore, I discuss some of the conceptual, methodological, and practical issues that have been put forward in the biological and psychological animal personality literature in recent years. I propose that with increased methodological care and clarity in reporting, the two fields can benefit one another. Thereafter, I highlight some areas of research in which common ground can be found and suggest prospects for future animal personality research.

5.2 Two Approaches to Animal Personality

Animal personality research is roughly dichotomized between the human-oriented personality psychological tradition and the animal-oriented biological tradition. The “psychological” and “biological” approaches to personality differ at conceptual, methodological, and practical levels.

The *psychological approach* is adopted by comparative personality psychologists who apply the well-established human personality theory and methodology to animal personality research. The aim is to understand similarities and differences in human and animal personality regarding the structure, underlying neuropsychological mechanisms, and evolutionary history. In humans, personality is understood as a psychological construct that influences behavior and is organized in a hierarchical structure (Maltby et al. 2007; see also, e.g., Allport 1961; Fast and Funder 2008 for

various definitions). According to the widely accepted Five-Factor Model (FFM), human personality consists of five stable superordinate domains or constructs labeled Extraversion, Openness, Conscientiousness, Neuroticism, and Agreeableness, each of which includes a number of subordinate facets (Costa and McCrae 1992; McCrae and Costa 2008; but see Eysenck 1991, 1992; Ashton and Lee 2007 for alternative models). Personality dispositions are heritable (Bouchard and Loehlin 2001) and associated with important life outcomes, such as subjective well-being, health, mortality, mating success, quality of social relationships, occupational performance, psychopathology, and the likelihood of serious injuries (Franken et al. 1990; Neeleman et al. 2002; Nettle 2005; Ozer and Benet-Martinez 2006; Roberts et al. 2007). Although traditionally the evolutionary significance and underlying mechanisms of human personality have received limited attention (Nettle 2006, 2008), advances have been made in recent years (e.g., personality genetics: Bouchard and Loehlin 2001; Ebstein 2006; Penke et al. 2007; brain substrates: Gardini et al. 2009; evolutionary significance: Nettle 2005, 2006; Smith and Blumstein 2008).

Some personality psychologists have become interested in comparative personality research and have described animal personality within the framework of human personality psychology (e.g., Gosling and Vazire 2002; Weiss et al. 2007; King et al. 2008). This has wide-ranging benefits for personality psychology research, such as clarifying the phylogenetic history of personality, as well as the effects of genetic dispositions, development, and environment that are challenging to tackle in research on humans alone (Gosling 2001; Gosling and Greybeal 2007). The concept of personality as a hierarchical psychological construct is extended to animal personality, with the expectation that animal personality exhibits a similar structural organization (e.g., King and Figueredo 1997). The framework of the FFM has been taken as the starting point, and the methods are adopted from those used in human personality research.

In human personality research, the most common method of obtaining data is self-rating, in which people evaluate themselves on lists of descriptive terms (“items”). However, assessment by knowledgeable informants (e.g., peers, parents, teachers) is also accepted and widely used (Boyle et al. 2008); and self- and other-rating can also be used in conjunction (e.g., Fast and Funder 2008). Assessing animals by knowledgeable informants (e.g., animal care-takers) is considered as a logical continuation of these methods (King and Figueredo 1997; Gosling and Vazire 2002). Thus, people rate animals on questionnaires that list descriptor items, which can be adjectives or behavioral descriptions, such as “curious” or “subject often touches new objects at great length” (Uher and Asendorpf 2008). So long as certain criteria – most importantly interrater reliability and construct validity (see definitions below) – are fulfilled, the results are considered to reflect subjects’ personality traits (Gosling and Vazire 2002; Vazire et al. 2007).

This work has revealed that personality of animals can successfully be characterized within the FFM framework (Gosling and John 1999; Gosling 2001; Capitanio and Widaman 2005). Personality constructs of animals vary in their degree of similarity to the human FFM, from highly similar (e.g., neuroticism in orangutans) (Weiss et al. 2006) to very different (e.g., dominance in chimpanzees) (King and

Figueredo 1997). This work has also led to further studies on heritability and cross-population consistency of ape personality and on apes' subjective well-being (Weiss et al. 2000, 2002, 2006, 2007, 2009).

The *biological approach*, as practiced by behavioral biologists, aims at finding out the mechanisms underlying, and the evolutionary forces maintaining, variation in personality traits. This approach builds on the traditions of ethology, behavioral biology, and evolutionary and theoretical ecology. Therefore, it relies on quantifying outward behavior. Whereas individual differences in animal behavior have been recognized as long as people have systematically observed animals (e.g., Yerkes 1939; Pavlov 1951; Stevenson-Hinde et al. 1980), in biological research variation was long considered the raw material for natural selection to act upon, rather than being adaptive in and of itself (e.g., Dall et al. 2004; Sih et al. 2004a, b; van Oers et al. 2005).

Variation around the assumed optimal mean was thought of as "noise" (Wilson 1998), and behavioral research aimed to find these optimal means for species, age, and sex categories. However, following increased interest in individual-based approaches and improved analytical methods, research has shown "noise" to be actively maintained by evolutionary processes (e.g., Dall et al. 2004; Wolf et al. 2007; Garamszegi et al. 2008; McNamara et al. 2009). This realization has led to efforts to quantify individual variation in behavioral traits. Usually behavioral personality research makes use of experimental testing, in which variation in a trait can be quantified by subjecting individuals to varying conditions or stimuli, such as a novel environment or a predator model (Réale et al. 2007). In addition, some biological personality research uses behavioral observations in natural or captive circumstances without experimental manipulation (Anestis 2005). Experimental and nonexperimental observations of behavior are coded to yield quantitative data on behavioral frequencies. This research has shown that in many species particular traits (e.g., aggressiveness, exploratory tendency, boldness, general activity) vary consistently among individuals (Sih et al. 2004b; Réale et al. 2007). Consistent variation is suggested to be maintained by frequency-dependent selection, mutation-selection balance, spatiotemporal variation in environmental conditions, and trade-offs between alternative strategies (Dall et al. 2004; Dingemanse et al. 2004; Wolf et al. 2007; Sih and Bell 2008; McNamara et al. 2009).

Largely, research on the evolutionary mechanisms of personality is still in its infancy, and much more additional theoretical and empirical work is needed to clarify the observed patterns in variation and consistency. What is clear, however, is that these findings have brought consistent individual differences into the focus of behavioral research. Recognition of the relevance of an individual as an explanatory level has large repercussions for studies on, for example, theoretical ecology, learning, cognition, mating behavior, and cooperation (Dall et al. 2004; Sih and Bell 2008; McNamara et al. 2009). Moreover, the concept of behavioral syndromes (i.e., consistently correlated behavioral traits) draws attention to limited plasticity in behavior, carry-over effects, and connections between behavioral traits that have traditionally not been studied together (Sih et al. 2004a, b; Sih and Bell 2008; Smith and Blumstein 2008).

The psychological and biological approaches have, at the outset, little in common. The gulf is further widened by the tradition of publishing in separate journals and attending different conferences. Consequently, the results are not easily comparable, and the advances in research in the respective fields often remain unrecognized by researchers taking different approaches. However, these approaches need not be so far apart.

5.3 Concepts in Personality Research: A Matter of Definitions and Analytical Levels

Conceptualization of personality in research is fundamentally a question of definitions and of the level of analysis. Nevertheless, it is by no means a trivial issue. Recently, Uher (2008a, b) highlighted it as one of the three critical issues of comparative personality research: how to conceptualize, identify the domains of, and measure individual variation.

The psychological and biological approaches to personality differ in their conceptualizations of personality. In the psychological tradition, the definition of personality allows multiple levels (psychological, situational, and behavioral) (Funder 2006). Conceptually, the trait hierarchy is emphasized, which demands knowledge of multiple traits and their relative externalizations. Personality is seen as a complex, hierarchical structure of narrow trait dimensions nested within broader trait dimensions. On the other hand, personality defined biologically, as consistent interindividual variation at the level of behavior, tends to ignore psychological influences and the hierarchical structure of traits (although the concept of behavioral syndromes is close to the concept of hierarchical structure in personality psychology) (Sih and Bell 2008; see also below). Although mechanisms are examined, they are not part of the definition of personality. Fundamentally, however, the differences between psychological and biological conceptualizations are minor, as both agree that personality describes stable interindividual variability in traits within a population (Sih and Bell 2008; Uher 2008a). The necessary criteria, consistency within, and variation between individuals can be assessed at any trait organizational level, including psychological dispositions (see discussions on trait organization in, e.g., Réale et al. 2007; Uher 2008a).

More problematic conceptual issues arise in comparative personality research, as species' biology strongly determines their behavior; consequently, comparing particular behavioral traits may lead to a "comparing apples with oranges" problem (cf. Gosling 2001). For example, an antelope's vigilance and easily triggered escape response may give an impression of a "shy" species if compared to a lion and a hornet's tendency to attack may give the impression of an "aggressive" species if compared to a sheep. However, the antelope's "shyness" and the hornet's "aggressiveness" result from particular ecological selection pressures leading to species-typical behavior. Within these species, aggressiveness and shyness can be characterized as personality traits if they exhibit greater between- than

within-individual variation that is sufficiently stable in a population. How, then, are we to compare the aggressiveness of hornets and sheep? Uher (2008a, b) proposed that we borrow conceptualizations for comparative personality research from cross-cultural personality psychology. That is, we should aim at identifying population-specific personality traits, weak universal personality traits, and strong universal personality traits. Population-specific personality traits are specific to a given species and thus cannot be compared across species. Universal traits are those that show consistent variation across species and are therefore comparable; strong universals are those that show significant differences between species' mean and variance of the trait distribution, and weak universals are those in which the mean and variance of the trait distribution are the same across species. When trait distributions differ among species, a mathematical standardization of the scores is necessary to allow comparisons.

The shyness–boldness continuum has been proposed as a universal trait due to substantial evidence of its existence in several species, including humans (Beaton et al. 2008; Sih and Bell 2008), but little is known of its trait value means and distributions across species. Uher's (2008a) framework is applicable to comparative research (but see Realo and Allik 2008). However, the framework puts little emphasis on how differences arise as a consequence of proximate determinants and evolutionary selection pressures. Even if a trait, such as boldness or aggressiveness, exhibits interindividual variation in a broad range of species, the proximate mechanisms may be different in different species. Moreover, the mean and variance of the trait distribution are likely to be strongly affected by species' ecology; consequently, particular traits are subjected to different selection pressures in different species. Therefore, in comparative research, identification of variation in a trait should ideally include determining proximate-level mechanisms and accounting for the species ecology and the selection pressures acting on the trait in the target species (Réale et al. 2007).

5.4 Methodologies in Personality Research

5.4.1 *How Are Candidate Personality Traits Selected, Extracted, and Analyzed?*

The methodological core issues concern how to (1) identify and (2) measure the domains of behavioral variation (cf. Uher 2008b). Identification, or selection, of candidate personality traits refers to the a priori process of deciding which traits are sampled as potentially personality-relevant ones. First, the definition and hierarchical level of a candidate trait are to be decided. One problem lies in the fact that the biological and psychological definitions of the term “trait” differ: Biologists understand a trait to be any (quantifiable) characteristic (see discussion of the term “characteristic” by Wagner 2001), whereas psychologists apply the term to internal

dispositions that influence behavior (Larsen and Buss 2005). Throughout this chapter, the term trait is used with its biological meaning and is limited to behavioral characteristics, following my focus on behavioral variation. Clarifying the definition of trait would reduce misunderstandings between the behavioral and psychological personality literature (see recent discussion of confusion about terminology by Carere and Maestripieri 2008; Uher 2008a, b; van Oers 2008).

The hierarchical level of the candidate trait is also relevant in the selection process. For example, maternal behavior is a composite trait consisting of nursing, carrying, protecting, grooming, and so on. These behaviors could be defined as individual traits or as measures of one composite trait. Each trait level is structurally connected to others below and above it (Réale et al. 2007). It depends on the question and the scale of the research on which organizational level the candidate traits are chosen. For example, if one is interested in behavioral syndromes, selection of candidates should include several lower-level traits that are examined for their interdependence, whereas if the goal is to identify fitness consequences of a particular trait, starting from a higher hierarchical level may prove more useful.

Uher (2008a) has summarized various approaches to selecting candidate traits. A “nomination approach” relies on the human ability to choose appropriate traits based on our perception of variation in animals, which allows a researcher to name the candidate traits. The better the species’ behavior is known, the more likely meaningfully varying behaviors are selected. An “adaptive approach” assesses the trait’s biological relevance in ecology or evolution of the species, so traits with the most significant fitness consequences in the past or present are assessed. A “top-down approach” takes personality traits found in other species and seeks similarities and differences in the target species. It can select a singular trait or base the selection on a broader hierarchical model of personality. Finally, a “bottom-up” approach starts from the study species and identifies candidates from its behavior or underlying mechanisms (see Uher 2008a, b for a thorough discussion).

Although this is an insightful categorization of the candidate trait selection approaches, some of these approaches are in practice close to each other and used in combination. For example, exploratory tendency and aggressiveness have been found to influence individual’s fitness in great tits (*Parus major*; Dingemanse et al. 2004), and consequently other studies have examined variation in these traits in other species (e.g., mouse lemur *Microcebus murinus*: Dammhahn 2009; dog *Canis familiaris*: Svartberg et al. 2005; guppy *Poecilia reticulata*: Burns 2008; starling *Sturnus vulgaris*: Minderman et al. 2009; collared flycatcher *Ficedula albicollis*: Gáramszegi et al. 2008). Selecting exploration tendency as a candidate trait in starlings combines the adaptive approach and the top-down approach and is possibly also influenced by knowledge that such behavior is part of the species’ behavioral repertoire thus adding the nomination approach to the list. Also, Weiss and Adams (2008) have pointed out that whereas rating animals on an adjective descriptor item list (for which the items were derived from the human personality model) utilizes personality traits of another species by the top-down approach, the item descriptions are often adjusted to each species’ particular behavioral repertoire, thus combining the top-down, bottom-up, and nomination approaches.

I combine and simplify Uher's (2008a) classification as mutually nonexclusive "know your species," "traits relevant in other species," and "compare to humans" approaches to candidate trait selection. The know your species approach relies on a broad knowledge base of the species' behavioral repertoire, socioecology, life history, and evolutionary history. When species' behavior has been sampled over years, in some cases decades, covering multiple individuals in multiple contexts and multiple populations, I consider it justified to select a range of naturally occurring behaviors as personality trait candidates. The benefit of this approach is that the selected candidate traits are likely to be ecologically relevant and part of the natural behavioral repertoire of the species. The drawback is a potential danger of selecting more easily accessible traits at the expense of rare or less conspicuous traits. The traits relevant in other species approach is an exploratory approach to test specific traits that have shown significance as personality traits in other species, either closely or more distantly related. The benefits of this approach are that it allows an assessment of the trait's phylogenetic history and mapping of the trait's generality across species (Gosling and Greybeal 2007). Also, it provides a time-saving shortcut to personality of a previously unstudied species. The most obvious drawback is that it may fail to account for traits relevant for the particular study species. Finally, the compare to humans approach seeks to identify those personality traits in animals that are known in humans, putting the focus on human–nonhuman similarities and differences. The drawback is that it may exclude traits that are absent in humans but biologically relevant for the target species (Uher 2008b; Uher and Asendorpf 2008; cf. Gosling and John 1999; Gosling 2001).

Based on ecological relevance and generality across species (i.e., know your species and traits relevant in other species approaches), Réale et al. (2007) nominated five categories for candidate personality traits in animals: shyness–boldness, exploration–avoidance, activity, aggressiveness, and sociability (see also Bell 2007). This proposition does not specify the genetic or neurophysiological mechanisms nor on which structural level at which the trait should be measured. These trait categories are likely to be ecologically and evolutionarily relevant regardless of the species' particular ecological conditions (Sih and Bell 2008). A possible drawback of keeping to these five categories is that it may limit research efforts to only these trait categories at the expense of other candidates. Moreover, in many species, some of these trait categories are correlated, suggesting structural dispositions among them (Sih and Bell 2008). Therefore, the five trait categories should not be presupposed to be independent.

All the aforementioned approaches have their own pros, cons, and justifications depending on the particular goal of the research. A common drawback in the outlined selection processes concerns the structural analysis. Understanding the structural hierarchy of personality traits is relevant because it clarifies the connections between traits and directs us to the mechanisms underlying these connections (Réale et al. 2007; Sih and Bell 2008). However, all selection processes necessarily limit structural analysis to the assessed traits only and may neglect other traits that are potentially more biologically significant for a given species. The traits relevant in other species approach identifies variation often only in one or two candidate traits

(e.g., boldness or aggressiveness) and disregards the structural organization altogether. The know your species approach may nominate easily observable traits in the target species' repertoire at the expense of less easily identified traits, again leading to a potentially incomplete structure. The compare to humans approach examines animals for those traits that are relevant for the human personality model, potentially biasing the structure toward that of humans. Furthermore, we must acknowledge that none of the selection methods produces an all-inclusive list of personality traits in any given species. For example, if boldness is identified as a personality trait in great tits, we cannot argue that we have found all there is to be found in great tit personality. Similarly, if human personality traits are used as a template to identify personality in chimpanzees, and subsequently some or all of these traits are shown to exhibit consistent variation in chimpanzees, it does not mean that chimpanzee personality only includes variation in those traits. So long as researchers are aware of the drawbacks and state clearly the reasons for and methods of their selection of candidate traits, comparisons with other studies are possible.

The second methodological concern is how the chosen traits are measured. The biological approach relies on coding expressed behavior. Biologists observe animals and extract quantitative data from these observations. The situation may be experimentally induced, or a trait may be coded in nonmanipulated living conditions in the wild or captivity. Once the candidate traits are chosen, appropriate paradigms for measuring the target trait are designed, and standard observational techniques are applied. For example, to test exploration tendency, an animal is put into a novel environment and its response is measured by, for example, latency to visit a particular part of the novel environment (Verbeek et al. 1994). To test boldness–shyness, a novel object is introduced into the environment, and the subject's latency to approach the object is recorded (Wilson et al. 1993). These tests are repeated over time for each subject. Data are analyzed for within- and between-subject variation and temporal consistency. In observations of nonexperimental situations, behavioral data of candidate traits are collected over a significantly longer period of time and across several contexts. The most common methods involve focal and scan sampling (e.g., Capitanio 1999; Uher et al. 2008). Precautions must be taken to avoid bias to particular individuals or to variation in behavioral patterns due to circadian rhythm and care-taking events by randomizing the order of focal individuals and observing every animal repeatedly at different times of the day and in several contexts, all of which are standard practices in behavioral research (Martin and Bateson 1993). To ensure that the sample is representative of real behavior, a sufficient amount of data from each individual and a rigorous observational technique are key criteria. Nevertheless, in nonexperimental settings, it may be difficult to obtain data for a particular trait as it occurs in nonsystematized contexts and is likely to be influenced by other factors than those we are interested in studying (Réale et al. 2007). On the other hand, observing behavior as it occurs without experimental stimulation avoids the problem of artificial or ecologically irrelevant situations.

The psychological approach relies on knowledgeable people rating the study subjects. The item lists consist of trait-relevant descriptors sometimes accompanied

by explanatory descriptions of the terms (e.g., Weiss et al. 2007). For example, the item “sympathetic” is given with an explanation “(s)ubject seems to be considerate and kind toward others as if sharing their feelings or trying to provide reassurance” (Weiss et al. 2006). Subjects’ item scores are analyzed for interrater reliability, which refers to agreement among raters in their assessment of a particular individual. The data are then subjected to data reduction methods (usually factor analysis or principal components analysis), which yield information on multiple traits and their taxonomic structure. The rating method relies on people’s intuitive ability to mentally collate and hold information of an animal’s characteristics in meaningful categories (Gosling and Vazire 2002; Uher 2008a). The benefit of this method is its practicality, as large numbers of animals can be sampled in a short time. In addition, cross-situational consistency and reliability are argued to be superior in the rating to that of the behavioral coding method because ratings incorporate information over time and contexts, whereas behavioral codings are necessarily more limited for time and are vulnerable to the influence of context (Vazire et al. 2007; see also below). However, the potential drawbacks of rating include unclear correspondence with behavior, unclear ecological relevance of rated items, and the ever-looming possibility of anthropomorphic projections (see below).

5.4.2 Diagnostic Criteria: Validity, Reliability, Repeatability

In Gosling’s (2001) comprehensive review on animal personality encompassing a broad range of species, more than 70% of animal personality research had relied on coding observed behavior. The rating method, however, was proportionately more often (42%) favored in studies on primates and domesticated animals. This reflects one of the key differences between the coding and rating methods: Rating animals is possible only when we can mentally represent an animal’s behavioral characteristics as impressions that translate to the descriptor items. This is likely to be easier when we find the behavior intuitively “understandable,” which is more probable in closely related species and species with which we have associated for a considerable part of human evolution (Gosling et al. 2003; Weiss and Adams 2008; Uher 2008b). It is thought that we hold less-clear representations of the behavior of animals that are taxonomically more distant from us or otherwise less familiar, and thus rating these animals with descriptive items enhances the risk of interpretational errors. Coding behavior, in contrast, is possible with any organism so long as there is an a priori agreement of what exactly is being coded (i.e., the definition of the behavior is clear).

The danger of anthropomorphizing animal behavior is present when we rate animals based on intuitive impressions and presumably more so when items are derived from human personality theory. The issue of anthropomorphism has been hotly debated in the animal personality literature, and it is beyond the scope of this chapter to summarize all of the arguments (e.g., Gosling and John 1999; Gosling and Vazire 2002; Itoh 2002; Réale et al. 2007; King et al. 2008; Uher 2008a, b). In

behavioral research, evaluating animals based on impressions of qualities labeled by human terms without quantified information of the corresponding behavior and its generality and frequency of occurrence is considered dubious. In contrast, the psychological research tradition puts little emphasis on behavioral frequency. Instead, the emphasis is in the psychometric properties of the emerging personality scores, which, when acceptable, are considered to reduce the likelihood of anthropomorphism. However, personality psychology is also well aware of the relevance of construct validity (i.e., the extent to which ratings reflect the corresponding real-life behavior and other corresponding and meaningful outcomes). Note that in this chapter the term “validity” is used as construct validity, and not face or concurrent validity, and convergent and discriminate validity is not separated – cf. Maltby et al. 2007. Construct validation is necessary to ensure that rated personality traits are reflected in quantifiable differences within the species’ behavioral repertoire (e.g., Gosling 2001; Uher and Asendorpf 2008). Yet, thus far, behavioral validation of ratings is not the standard procedure (Gosling 2001).

Animal personality studies that have assessed construct validity have generally reported high correspondence between ratings and observed behavior (Feaver et al. 1986; Pederson et al. 2005; Konečná et al. 2008). In a study on rhesus macaques (*Macaca mulatta*), behavioral scores correlated moderately with the corresponding rated scores (Capitanio 1999). Moderate to high correspondence was also found in two studies on captive chimpanzees (*Pan troglodytes*) (Pederson et al. 2005; Vazire et al. 2007); but in another study (Uher et al. 2008) where behavioral data were obtained both experimentally and nonexperimentally, the correspondence between rated adjective-item data and coded behavioral data was low. Sometimes the obtained validity results are difficult to evaluate owing to biological or methodological challenges. In a thorough study on wild-ranging male Hanuman langurs (*Semnopithecus entellus*), ratings corresponded well to measured behavior, and the principal components analysis (PCA)-derived personality dimensions obtained by behavior coding and ratings agreed with each other (Konečná et al. 2008). However, coded and rated scores were influenced by male rank, which in langurs is labile (i.e., the rank position changes during the lifetime) (Borries 1997). This evokes a question regarding to what extent currently observed behavior is consequent of (unstable) rank position rather than personality. Furthermore, how do personality and rank position interact? As short-term studies are snapshots in time, the causal relations between rank position, behavior, and personality are difficult to assess. A methodological issue is the independence of rating and behavior coding; to truly test the construct validity of ratings, the behavioral data should be obtained independently (i.e., by different people), but this has not always been the case (e.g., Feaver et al. 1986; Capitanio and Widaman 2005; Konečná et al. 2008). Validations have also been done by rating observed behavior, rather than quantifying frequency, duration, and so on of the target behaviors (Gosling et al. 2003), and have been based on limited sampling efforts (Vazire et al. 2007). Finally, researchers may rely on the assumption that if someone has validated (some of) the personality traits in the same species (even if in a different population), it is unnecessary to perform behavioral coding (e.g., Weiss et al. 2002; King et al. 2008). Although cross-population

rating studies give converging results supporting the generality of personality (King et al. 2005; Weiss et al. 2007, 2009), the actual behavioral frequencies may well differ among populations. In sum, the importance of rigorous behavioral validation cannot be overemphasized. As a standard procedure, it would provide data with a common metric (i.e., occurrences and frequencies of strictly defined behavioral traits) that not only would facilitate comparisons across populations (and potentially across species), thus complementing data obtained by ratings, but also comparisons with behavioral personality studies. By including quantified behavioral measures of rated personality, it is possible to assess directly the similarities with studies conducted by behavioral coding.

In contrast to ratings, the problem of construct validity is less of an issue in behavioral coding as the actual behavior is quantified. Behavioral research is not free from validation challenges, as there is always an *a priori* expectation of the correspondence between the target personality trait (e.g., shyness) and the behavior (e.g., latency to approach an object), which may or may not be a correct assumption. To ensure construct validity in behavioral research, knowledge of the species' behavioral repertoire and the functions of measured behaviors are imperative. Furthermore, some researchers (Vazire et al. 2007) have raised a concern that observers may interpret behavior wrongly (e.g., code submissive behavior as play), which would undermine the value of behavioral coding. Of course, as in any behavioral research, coders must be trained well to be familiar with a species' behavior so they recognize the traits they code and record the observations reliably (see below for discussion on reliability). If knowledge of species' behavior and functions of target traits, as well as coders' sufficient training in recognizing and obtaining behavioral data are ensured, I consider construct validity of behavior coding to be, by default, high.

Biologists stress the importance of another kind of validity, namely ecological validity (Réale et al. 2007; Burns 2008). That is, the test design and the behavioral measures should be ecologically relevant for the species. For example, a novel object that an animal reacts to is likely to be different for a bird than for a fish. Furthermore, response in a test should translate into responses in the corresponding real-life situation. In a recent study, mouse lemurs exhibited personality variation in standard novel object and open environment tests designed to assess variation in boldness and exploration tendencies (Dammhahn 2009). However, when the same animals were tested in a realistic situation posing varying degrees of risk – feeding on the ground (risky situation) versus feeding on a higher platform (safe situation) – the responses were not attributable to the measured personality differences. The author hypothesized that exploration tendency and boldness do not influence the survival component of fitness in this species. Alternatively, the test situation may not tap into personality differences exhibited in the real-life situation, thus illustrating the potentially low ecological relevance of the standard tests for this species. To ensure salience of the test situation, experimental setups should account for species' ecology and natural behavior. In addition, traits ideally are assessed by several tests on the same trait (Burns 2008). In nonexperimental studies, ecological validity is vulnerable to the effects of context (Weiss and Adams 2008), which can

be overcome by sufficient sampling efforts. In rating studies, the ecological validity may be left implicit (Uher 2008a), especially for terms that have a less clear behavioral meaning. However, ecological validity can be ensured by showing that the rated items have an equivalent in naturally occurring behavior.

Another key criterion is sufficient reliability (i.e., agreement in assessment between raters/coders) to minimize the chance of rater and coder biases. In rating studies, this is ensured by multiple raters whose assessments are tested for correlation. The items that do not meet the criterion are excluded from further analyses. Rating studies have shown remarkably high interrater reliabilities in various species, reflecting a high agreement between people on the animals' characteristics (or, rather, between peoples' impressions thereof) (Gosling 2001). However, interrater reliabilities are shown to be lower for items that have a behaviorally less clear connotation – such as eccentric, jealous, sensitive – compared to items that are behaviorally clearer, such as dominant, aggressive, and playful (Gosling 2001; Vazire et al. 2007; Dutton 2008). Reliability in rating thus seems to at least partly depend on how behaviorally clear the semantic meaning of the item descriptor is. Behavior coding studies have been noted for having low reliability or for not reporting reliability (Vazire et al. 2007). Indeed, reliability is often not tested or reported in behavioral personality studies, leaving unclear how many people coded the behavior and whether interobserver reliability was tested. This is in contrast to behavioral research outside of the personality realm, where testing for interobserver reliability is a standard procedure (observational research: e.g., Parr et al. 2005, Koski et al. 2007; experimental research: e.g., Call et al. 2005, Silk et al. 2005). The absence of reliability reporting in behavioral personality research is unfortunate. It remains crucial that interobserver reliability is habitually assessed in personality studies that rely on behavioral coding.

To solve the debate between coders and raters as to which approach is better in animal personality research, Vazire et al. (2007) conducted a study using both methods. A total of 52 captive chimpanzees were rated on a 34-item list (a subset of item lists used in research on rhesus macaque and spotted hyena personality by Capitanio 1999 and Gosling 1998, respectively), as well as coded on a range of behaviors by one observer, obtaining 2–3 h of behavioral data per chimpanzee. The resulting scores of rated items and a selected subset of observed behaviors were correlated. The level of agreement between rated items and coded behavior per conceptually equivalent category varied greatly, from negligible to highly significant, implying that impressions on behavior and quantification of the corresponding behavior did not consistently match. Reliability of the rated data concerned, as is customary, the interrater correlation of the rated item scores. This was high, indicating that people shared their impressions about the chimpanzees' personality. In contrast, the reliability of the coded data was tested by treating each 15-min focal observation of a chimpanzee as an independent observation, which was correlated with other singular focal samples of the same chimpanzee (allowing calculation of the intraclass correlation coefficient). However, this procedure hardly represents good behavioral research practice for two reasons. First, a total of 2–3 h of observation of a mammal with a complex behavioral repertoire is a very limited sample of

its general behavior patterns. Second, one focal observation cannot be considered as an independent and representative sample of an animal's overall behavior. With small sample sizes, the risk of over- or underestimating behavioral parameters is considerably inflated (Martin and Bateson 1993). Moreover, testing intraclass correlations of singular focal samples is not an equivalent reliability test to inter-rater agreement in rating. To obtain a reliability measure comparable to the one of rated items, behavioral observations of several people obtained simultaneously should have been compared to each other.

In sum, rating studies often suffer from a lack of independent and quantitative behavioral validation, which also leaves the ecological relevance of (some) rated items unclear. Coding studies have potential for a high construct and ecological validity, depending on the trait selection, experimental procedures, and sampling effort. Reliability among raters/observers is usually high in rating studies, whereas in coding studies it thus far is often left untested.

Yet another diagnostic measure of a personality trait is repeatability or consistency over time. Behavioral consistencies have been analyzed in many ways (Hayes and Jenkins 1997). The current standard in behavioral research is to calculate a trait's repeatability (i.e., an estimate of the variation within and between individuals). Repeatability is calculated with an analysis of variance (ANOVA), with individuals as a fixed factor and with a minimum of two measures of a trait for each individual (Lessells and Boag 1987; Bell et al. 2009). Behaviors that show low within-individual variation but high between-individual variation are more repeatable. In a recent meta-analysis, Bell et al. (2009) showed that across a large range of taxa and behaviors the average repeatability was significantly greater than 0, although there were species and sex differences. Individual differences accounted for roughly 37% of the variation. Also, psychological studies on animal personality have used various methods to test temporal consistency – for example, Cronbach's alpha (Uher et al. 2008) and intraclass correlation coefficients (e.g., King and Landau 2003), which is statistically identical to repeatability. Thus, the importance of behavioral consistency is agreed upon in both approaches.

5.5 Finding Common Ground

This chapter focuses on the differences between the psychological and biological approaches to animal personality. I have also stressed that it is possible to overcome the differences by appropriate methodological practices and improved clarity in reporting. Below are some aspects that I believe are of interest to both psychological and behavioral personality research and that would likely benefit from communication across disciplines.

Noted earlier is the importance of hierarchical structure in the psychological personality research tradition, which is largely ignored in the behavioral research tradition. However, as behavioral syndromes are now in the forefront of behavioral research (cf. Sih and Bell 2008), they directly link with the question of structure of

personality traits. Which personality traits form syndromes and whether those syndromes are conceptually similar to constructs from the human personality theory are interesting avenues for future research. We also need to understand whether and when behavioral correlations are stable and which mechanisms underpin them. Understanding how multiple behavioral syndromes influence overall behavior and how they are dependent on each other is important in its own right (cf. Sih and Bell 2008), but unraveling structural hierarchy of animal personality also allows direct comparisons with human personality structure.

Animal and human personality research would make significant advances by addressing the four questions posed by Tinbergen (1963): causation, function, ontogeny, and evolutionary history (Bell 2007; Nettle 2008). Causation of behavior is about the proximate mechanisms underlying behavior. Both biological and psychological work has revealed a number of interesting mechanisms of personality. The genetic base of personality has been confirmed by establishing a significant heritability of numerous traits (Bouchard and Loehlin 2001). Direct connections between certain personality traits and their genetic and neurochemical correlates have also been proposed – for example, between a polymorphic dopamine receptor gene (*DRD4*) and novelty-seeking behavior (Roussos et al. 2009; but see Klueger et al. 2002) and between a serotonin transporter gene (*5-HTT*) and anxiety-related traits (Ebstein 2006) in humans. Several other neuropeptides and hormones have been connected to personality, including testosterone (androgen receptor polymorphism: Westberg et al. 2009; circulating testosterone: Rowe et al. 2004), vasopressin (Bartz and Hollander 2006), and cortisol (Hauner et al. 2008). Polymorphisms in the *DRD4* and *5-HTT* genes have also been identified in some animals, including nonhuman primates (Livak et al. 1995; Seaman et al. 2000; Bailey et al. 2007; Inoue-Murayama et al. 2008), and they may influence their personality traits much as in humans (Inoue-Murayama et al. 2006, 2008; Bailey et al. 2007; Spinelli et al. 2007; Inoue-Murayama 2009). Establishing the genetic and physiological bases of human personality is one of the key challenges in human psychology (cf. Penke et al. 2007), and animal models are an important part of this work. However, it is equally important to establish mechanisms of animal personality in their own right. Illuminating links between genetics, brain functions, behavioral endocrinology, and personality traits is important to advance our understanding of both human and animal personalities for fundamental and applied reasons.

The fitness consequences of and the evolutionary mechanisms maintaining human personality are gaining attention (MacDonald 1995; Nettle 2005, 2006, 2007; Penke et al. 2007). As empirical research on the costs and benefits of personality in humans is still limited, it can benefit from the active research on these questions in animal personality research. Identifying fitness consequences of personality traits is one of the main goals of biological personality research. It has been shown that many heritable personality traits have significant fitness consequences in terms of reproductive output and survival (Dingemanse and Réale 2005; Smith and Blumstein 2008). This has evoked a new set of questions about the evolutionary significance of personality. For example, most animal studies have addressed the fitness effects of single traits but not of correlated traits (Smith and Blumstein 2008; but

see Sih and Watters 2005). How the different organizational levels of traits influence the overall behavior and how they influence individual's fitness are interesting future questions. Also, although some aspects of the environment's influence on fitness consequences of animal personality have been shown (e.g., spatiotemporal variation in resource availability) (Dingemanse et al. 2004), there is much to be done to unravel the role of environmental conditions – e.g., predation pressure, social conditions, fluctuations therein – in determining fitness effects of personality traits (Sih and Bell 2008).

Studying personality in social species is an especially interesting direction of research as some have suggested that social environments promote consistency in behavior (Fishman et al. 2001; Dall et al. 2004; McNamara et al. 2004) and maintain interindividual variation in continuous behavioral traits through frequency-dependent selection (McNamara et al. 2009). Social environments also influence how personality traits manifest. For example, in rainbow trout (*Oncorhynchus mykiss*) observations of another's shyness made bold individuals shyer, whereas shy individuals became bolder (Frost et al. 2007); and among zebra finches (*Taeniopygia guttata*) individuals' exploration tendency increased in the company of an exploratory individual (Schuett and Dall 2009). In addition to the effects of the social environment on the manifestation of personality traits in general, sociability as a personality trait has been surprisingly little studied in animals. In the common lizard (*Lacerta vivipara*), individual variation in sociability has been shown to influence survival and reproductive success (Cote et al. 2008). Similar, but indirect, evidence comes from primates: Baboon (*Papio cynocephalus*) females' social network size correlates positively with their fitness (Silk et al. 2003, 2009). Whether and how network size is dependent on personality in baboons is unknown. However, in young rhesus macaques, personality (i.e., activity and calmness) predicts the number of social relationships (Weinstein and Capitanio 2008). In chimpanzees (Anestis 2005) and vervet monkeys (*Chlorocebus aethiops*) (Fairbanks et al. 2004), some personality traits (i.e., aggressiveness and reactivity in chimpanzees, impulsivity in vervets) predict male rank, thus influencing males' fitness. Furthermore, differences in chimpanzee alpha males' dominance "styles" regarding their social grooming patterns have been identified, likely reflecting differences in personality traits (Foster et al. 2009), but it is yet unknown whether they have consequences for their fitness.

Humans, like most other primates, are a highly social species. In human personality, sociability is, like excitement-seeking, a facet of extraversion (Costa and McCrae 1992), which is shown to predict sexual promiscuity (Schmitt 2004; Nettle 2005) and social network size (Swickert et al. 2002). Furthermore, sociability has been shown to increase the likelihood of having children (Jokela et al. 2009). These findings indicate that sociability has evolutionary relevance in us as well. Therefore, the social environment, the particular personality traits it favors and constrains, and its influence on fitness are intriguing questions for human and animal personality research.

Ontogeny of human personality has traditionally been the realm of developmental psychology. Personality during early years is often referred to as temperament (McAdams and Olson 2010). The continuity from temperament to the five

personality constructs has been scarcely studied, although some studies have proposed a developmental scheme from the early temperament dispositions to personality factors (reviewed by Caspi et al. 2005; Rothbart 2007; McAdams and Olson 2010). Later in life, personality develops in predictable ways: mean trait levels of neuroticism decrease, agreeableness and conscientiousness increase, and openness first increases and then decreases during adult life (Roberts et al. 2006). Early ontogeny and later development of personality traits has barely been studied in animals (cf. Stamps 2003). King et al. (2008) described the development of personality constructs in chimpanzees as nearly identical to that of humans. In three-spined stickle-backs (*Gasterosteus aculeatus*), boldness and aggression were stable through individual development in one study population but not in another (Bell and Stamps 2004). For great tit nestlings, handling stress (i.e., fear response to being handled by a human) at the age of 14 days correlated with the response 6 months later (Fucikova et al. 2009). Developmental aspects in animal personality deserve more research as the age-related changes in animal personality are poorly understood. Moreover, they can illuminate the effects of gene–environment interactions on personality (cf. Caspi et al. 2005; Roberts et al. 2007).

Finally, research into the evolutionary history of personality traits will benefit the most from comparative personality research and thus from an integrative phylogenetic framework (Gosling and Greybeal 2007). The process of identifying similarities and differences in personality across the animal kingdom, including humans, has only just started. Some personality traits, such as exploration tendency and boldness, appear to be important for a whole host of species and analogous (or homologous) with human personality traits within the constructs of openness and extraversion, respectively (Gosling and John 1999; Beaton et al. 2008). However, we are far from understanding how personality traits have evolved in various taxa, which of the similarities are due to homology and which to convergence, how the differences can be explained, and how this relates to a range of other aspects, such as species' life history, population dynamics, cognition, learning, and social structure, to name but a few. Animal personality research is coming of age, and as it grows it will significantly affect our understanding of human and animal behavior. The first tentative steps toward a unified approach to animal personality have been set. Aligning the concepts in animal personality research by different approaches will greatly enhance the advances in this rapidly growing field of research.

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